

Relationships between coarse woody debris habitat quality and forest maturity attributes

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Abstract

Coarse woody debris (CWD) is an important contributor to forest biodiversity because it provides essential habitat for saproxylic (dead wood-dependent) species. However, CWD is frequently overlooked in forest management and restoration decisions around the world. We have therefore developed an index of CWD habitat quality that integrates four important characteristics of saproxylic habitat. We apply this index to wet eucalypt forests in Tasmania, Australia. The relationships between the CWD index and standing forest structural and floristic maturity metrics were weak ($R^2 < .09$), highlighting the necessity to explicitly factor CWD habitat into conservation planning. A hump-shaped relationship between current CWD habitat quality and variables linked to future quality (standing tree basal area and the number of old-growth eucalypts) implies that stands with medium current quality provide better potential future habitat than stands with high current quality. CWD habitat quality was lower in previously harvested stands. We present a web app that calculates CWD habitat quality scores from raw field measurements. Our approach can be applied in conservation assessments to determine habitat availability for biodiversity, and to quantify the impacts of management actions and restoration activities.

KEYWORDS

clear-cutting, dead wood, downed woody debris, index, restoration, saproxylic, silviculture, sustainable forest management, wildfire

1 | INTRODUCTION

Coarse woody debris (CWD) provides critical habitat for saproxylic (dead wood-dependent) species in forests worldwide (Grove, 2002). Many invertebrates, fungi, bryophytes, epiphytic plants and vascular plants, including numerous rare and threatened species, rely on CWD as the sole habitat for all or part of their lifecycle (Gates, Mohammed, Wardlaw, Ratkowski, & Davidson, 2011; Grove & Stamm, 2011; McGee & Birmingham, 1997; Siitonen, 2001; van

Galen, Baker, Dalton, & Jordan, 2016). Saproxylic species form a substantial part of global forest biodiversity (e.g., at least 20–25% in Finland; Siitonen, 2001), and account for a considerable component of red-listed species (e.g., approximately 25% in Sweden; Jonsson et al., 2006). Timber harvesting can have large impacts on CWD habitat availability and dynamics, with long-lasting impacts on saproxylic biodiversity (Grove & Meggs, 2003). As well as the removal of standing trees (thus reducing future CWD inputs), many harvesting practices also remove downed

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“waste” wood for use as fuel wood, impacting current habitat availability for saproxylic biodiversity (Grove, 2009; Riffell, Verschuyt, Miller, & Wigley, 2011). There is an increasing recognition of the importance of CWD, including deliberately creating CWD habitat in restoration programs (Manning, Cunningham, & Lindenmayer, 2013). However, tools to enable conservation practitioners to assess CWD habitat quality are generally lacking. Because of the close associations between biodiversity and CWD, measuring and integrating important CWD attributes can provide a simple, cost-effective proxy for determining habitat availability for saproxylic biodiversity and assessing impacts of management actions and effectiveness of conservation programs.

Despite the contribution of CWD to forest biodiversity, CWD is rarely incorporated into forest management protocols around the world, with forest management decisions predominantly focused on forest age or successional stage. Forest containing greater proportions of mature structural and floristic characteristics (such as larger trees and late-successional vascular plant species) are generally considered to possess greater habitat value, and are often prioritized for reservation (Baker et al., 2019; Lindenmayer & Franklin, 2002; van Galen et al., 2018). Whether these forests also contain habitat for saproxylic species relying on good quality CWD is poorly understood (Moroni, Musk, & Wardlaw, 2017; Ulyshen, Horn, Pokswinski, McHugh, & Hiers, 2018). It is possible that CWD dynamics may be disconnected, or experience time lags, from attributes of standing forest condition (Manning et al., 2013; Siitonen, 2001). Previous reviews have highlighted that the lack of inclusion of information on CWD in many current management protocols is a major cause for concern (Grove, 2002; Grove & Meggs, 2003; Siitonen, 2001).

There is a lack of systematic approaches for assessing CWD habitat quality around the world (Grove & Meggs, 2003; Müller & Bütler, 2010). Although line intersect transects are often used, current assessment methods are either focused on only one aspect of CWD, such as volume (Davis, Belote, Williamson, Larson, & Esch, 2015; Gibbons & Freudenberger, 2006; Waddell, 2002), carbon stocks (Woodall, Heath, & Smith, 2008), or decay stage (Pyle & Brown, 1998; Woldendorp, Keenan, Barry, & Spencer, 2004), or are designed for specific species from a specific region (Jonsson et al., 2006). To be of use for management planning, a generalized index that incorporates multiple characteristics important for saproxylic habitat would be beneficial. While detailed knowledge of saproxylic fauna and flora is lacking for many forest systems, research has highlighted that certain CWD characteristics directly affect saproxylic assemblages; particularly size, amount, decay stage, tree species and continuity through space and

time (Grove, 2002; Grove & Meggs, 2003; Harmon et al., 1986; Siitonen, 2001; Wardlaw et al., 2009; Yee, Yuan, & Mohammed, 2001). Specifically, large logs often contain higher abundances of species (particularly unique species) and different fungal decay communities compared with smaller logs (Grove & Forster, 2011; Yee, Grove, Richardson, & Mohammed, 2006). The amount of CWD available has been linked to saproxylic species richness and impacts the survival of dispersal-limited species (Grove, 2002; Ranius & Jonsson, 2007). Additionally, many species are specialists of particular decay stages (Jonsell, Weslien, & Ehnström, 1998; Renvall, 1995). Therefore, incorporating the attributes of CWD that are important for habitat quality into a generalized metric could provide valuable information about the overall health of the saproxylic community (Grove, 2002). While integrating CWD quality into a single metric might be an oversimplification for situations requiring detailed information for certain species, such simplifications would be valuable for site-based assessment of overall habitat quality.

CWD dynamics vary depending on the rate of inputs (fallen trees or dropped branches) and outputs (decay or removal). Inputs and outputs rarely reach equilibrium in forests subjected to sporadic disturbances, such as wildfires, windstorms, insect outbreaks or timber harvesting (Grove, 2002; Siitonen, 2001), but may be more stable in forests subject to small gap phase disturbances. Disturbances add large amounts of CWD into the system, after which these inputs slowly decay and new input slows. Post-disturbance inputs come from many sources including fallen branches and trunks of trees that survived the disturbance, self-thinning of regenerating trees, and dead wood created by invertebrates, fungi, diseases, or drought (Franklin et al., 2002; Grove, Stamm, & Barry, 2009; Harmon et al., 1986; Spies, Franklin, & Thomas, 1988). Although general patterns exist, post-disturbance trajectories of CWD development are highly variable and depend on many things including the pre-disturbance forest structure, the regularity, intensity and severity of the disturbance, and climatic factors. The complexity of CWD dynamics mean the characteristics of the CWD cohort may be only weakly related to other elements of stand structure, including elements that are important for the future formation of CWD (Muller & Liu, 1991; Nilsson et al., 2002). Therefore, as well as assessing the current quality of CWD habitat, it is important to consider the potential future quality contained within the standing wood. The most appropriate variables and spatial scales to consider may vary between forest systems, due to differing dynamics of CWD formation and decay.

The type of disturbance plays a particularly important role in CWD formation. Legacy trees remaining after disturbances such as wildfires lead to continued input of fresh, large-diameter CWD of varying decay stages. Conversely,

high intensity disturbances such as hurricanes, or forest management practices like clear-cutting, produce greater initial volumes of CWD but leave little remaining standing structure (Grove & Stamm, 2011). After the initial wood decays, the lack of legacy trees means input is slow and certain habitat characteristics such as large, old-growth logs and wood during early stages of decay can become very rare (Siitonen, 2001; Sippola, Siitonen, & Kallio, 1998; Thauvin, Libis, Grove, & Wardlaw, 2010). The lack of old-growth CWD can be particularly problematic for many species, as old-growth wood provides unique habitat for many specialist species (Yee et al., 2006). Therefore, standing old-growth trees play an important role in the future quality of CWD.

In this study, we develop an index of CWD habitat quality using the most important variables influencing saproxylic habitat. We use this index to examine the relationship between CWD habitat quality and structural and floristic forest maturity in a well-studied forest system; wet eucalypt forests in Tasmania, Australia. We also examine the relationship between current CWD habitat quality and future quality, and compare CWD quality in harvested (clearcut) and unharvested (wildfire-origin) stands. We also present an app suitable for web browsers that calculates index scores for new sites from raw field measurements, and that can be adjusted to suit other forest systems around the world by calibrating with region-specific reference data. The index and app are particularly important because of the general lack of methods for assessing CWD habitat quality. This study provides important information on whether current management protocols based on mature attributes are adequate to conserve saproxylic habitat, or whether greater consideration of CWD in managed forest ecosystems is required.

2 | METHODS

2.1 | Data collection

We measured CWD characteristics at 68 sites in wet eucalypt forest in southern Tasmania, Australia (see site map in Data S1). Sites were selected using a stratified random approach to span a wide range of forest developmental stages, from 20-year-old regeneration to old-growth (see van Galen et al., 2018 for further details). Mean annual rainfall for the sample sites ranged between 800 and 1,700 mm (Australian Bureau of Meteorology, 2017), and elevation from 60 to 821 m above sea level. Thirty-four of the sites were silvicultural regeneration that had been clearcut between 1961 and 1997 and then burnt with high intensity fire. The remaining 34 sites were wildfire-regeneration and had not been harvested with modern methods, although approximately one third had been subjected to very low intensity pre-1960s selective logging.

At each site, we sampled one 200 m transect along a random bearing using the line intersect method (Van Wagner, 1968). To avoid edge effects, the transects were at least 25–200 m from any roads or harvest boundaries. We measured the height and width of each piece of downed CWD >10 cm in diameter where intersected by the transect. Most pieces were whole fallen trunks or branches, but some were fragmented logs. Standing dead trees were not included. As CWD generally decays asymmetrically to form an oval shape (rather than remaining cylindrical), the longest measurement was used as the diameter. Each piece was also assigned a decay class ranging from 1 to 5 using the methods of Woldendorp et al. (2004) (Data S1). The CWD originated from numerous canopy and understorey tree species; mostly *Eucalyptus* spp., *Nothofagus cunninghamii*, *Atherosperma moschatum*, *Eucryphia lucida*, *Phyllocladus aspleniifolius*, *Pomaderris apetala* and *Acacia* spp. We were unable to identify the species of all individual logs.

We also measured two variables that are strongly linked to the future formation of CWD; the number of standing “old-growth” eucalypts (large trees with irregular crowns beginning to senesce, and also large dead trees), and the stand basal area of all live and dead trees. The number of old-growth eucalypts is linked to the potential number of large logs and types of decay that will be present (Wardlaw et al., 2009; Yee et al., 2001). The basal area indicates the overall amount of wood available to form future CWD, assuming the stand is not harvested. Basal area was calculated by measuring the diameter at breast height (DBH) of all trees present in four 12 m radius circular plots evenly spaced along the 200 m transect. Due to their rarity, larger trees (DBH > 75 cm) were also measured in 20 m radius plots established around each 12 m radius plot. Using the tree form-class classification system described in van Galen et al. (2018) (Data S1), we classified eucalypts as either “old-growth” (form Classes 2–10) or “regrowth” (form Class 1). While these variables are the most relevant for wet eucalypt forests, other variables may be more appropriate to consider in other systems, depending on the dynamics of CWD formation and decay.

2.2 | Creating the CWD habitat quality index

To quantify CWD habitat quality, we developed an index using four variables created from the data collected along the line intersect transects: (a) the maximum diameter, (b) the diameter median, (c) the number of pieces, and (d) a statistic of decay class evenness. These four variables were selected based on published literature and expert opinion, and were chosen because they cover the attributes most important for saproxylic habitat (size, amount and decay), have well-documented positive relationships with habitat

TABLE 1 The four variables included in the index

| Variable | Details | Relationship with habitat quality | Examples |
|----------------------|--|--|--|
| Maximum diameter | The diameter of the largest piece of CWD on the transect (square-root-transformed) | Large, old-growth CWD supports more saproxylic species than smaller CWD, including more unique and obligatory species. Large logs also decay differently to smaller logs (from the inside out as well as the outside in), and contain different fungal decay communities. The presence of at least one large log has a big influence on the saproxylic community composition | Sippola et al. (1998); Yee et al. (2006); Wardlaw et al. (2009); Gates et al. (2011); Grove and Forster (2011) |
| Diameter median | The median diameter of all CWD pieces along the transect | Larger CWD supports more saproxylic species than smaller CWD, due to greater volume and surface area | Väisänen, Biström, and Heliövaara (1993); Heilmann-Clausen and Christensen (2004); Lachat et al. (2006); Ranius and Jonsson (2007); Grove and Forster (2011) |
| Number of pieces | The number of CWD pieces encountered along the transect (square-root-transformed) | Stands with more CWD pieces support more saproxylic species due to increased habitat availability. More pieces also lead to more spatial connectivity, which is an advantage for dispersal-limited species | Siitonen (1994); Økland, Bakke, Håggvar, and Kvamme (1996); Schiegg (2000); Ranius and Jonsson (2007) |
| Decay class evenness | The total deviation from equal numbers of CWD in each decay class, standardized by the number of CWD (see Section 2) | Each decay class has specific characteristics, so a more even distribution of decay classes leads to more diversity of habitat available for saproxylic species | Renvall (1995); Jonsell et al. (1998); Küffer and Senn-Irlet (2005); Lachat et al. (2006); Gates et al. (2011) |

quality (Table 1) and were not strongly correlated with each other ($r < .28$). Both the maximum diameter and the diameter median were included as these capture different aspects of CWD size; the median indicates the overall size of the CWD cohort, whereas the maximum indicates the presence of very large logs, which provide particularly unique habitat (Yee et al., 2001). Although volume is commonly used to describe CWD, we did not include this variable because most information described by volume is captured by the more ecologically relevant maximum and median diameter variables. Decay class evenness was calculated for each site according to this formula:

$$\frac{-\sum |n - \frac{N}{5}|}{N},$$

where n is the number of logs in a decay class and N is the total number of logs in that site. Σ represents the sum across the five decay classes. The negative sign ensures a positive relationship with habitat quality.

We square-root-transformed the maximum diameter and number of pieces, as a unit change in these variables is likely to be more ecologically significant at the lower end of the variable gradient than at the higher end (unlike changes in

diameter median and decay class evenness). We chose this transformation to be consistent with our knowledge of ecological processes underpinning the habitat quality of these variables. However, indices created using other transformations (untransformed, log and fourth-root) were highly correlated with the preferred index ($r > .997$) indicating that the choice of transformation has little impact.

To create the index, the four variables were standardized (mean = 0, $SD = 1$) and summed. The totals were then standardized to range between 1 and 100. We used “R Shiny” (Chang, Cheng, Allaire, Xie, & McPherson, 2015) to create a web-browser app that computes index scores from raw data collected at new sites based on the parameters of our reference data set. Alternative reference data sets from other forest systems can also be uploaded to calibrate the app for use in other regions.

During sampling, CWD were recorded within 50 m subsections of the 200 m transect to test the optimal transect length required to accurately capture stand characteristics. Our choice of 200 m appears to be sufficient, as reducing the transect length to 150 m only marginally altered the index scores ($R^2 = .91$). Further details and results of this analysis are provided in Data S1.

2.3 | Statistical analysis

2.3.1 | CWD quality and forest maturity

To examine the capacity of forest maturity to act as a proxy for CWD quality, we used Generalised Additive Models (GAMs) from the “mgcv” package (Wood, 2011) in R (R Core Team, 2018) to model the relationships between CWD habitat quality and forest maturity. We modeled both the CWD index and the individual CWD component variables against the structural and floristic maturity metrics created for the same sites in van Galen et al. (2018). We used negative binomial error distributions for models involving the number of pieces and Gaussian for all other models. The smoothing parameter was set at $k = 3$. These decisions were made by examining the diagnostic plots produced by the “gam.check” function, and where appropriate, boxcox plots from the “MASS” package (Venables & Ripley, 2002). Maximum diameter was square-root-transformed and median diameter was transformed to the power of -1 . Transformed variables were back-transformed to plot the relationships.

2.3.2 | Current versus future quality and the effect of harvesting

We also used GAMs as described above to model relationships between the CWD index and the two stand structural variables describing potential future formation of CWD: the number of old-growth eucalypts and the stand basal area. A negative binomial error distribution was used to model the number of old-growth eucalypts and a Gaussian error distribution to model the basal area. The basal area was log-transformed to run the model, then back-transformed to plot the relationship. We performed these analyses separately for wildfire-regenerated sites and clearcut-regenerated sites. We also performed Mann–Whitney U tests to determine whether index scores, the number of old-growth eucalypts and stand basal area differed between disturbance type (wildfire-regenerated vs. clearcut-regenerated).

3 | RESULTS

A wide range of CWD characteristics were captured within the sites; the maximum diameter ranged from 57 to 280 cm, diameter median from 15.8 to 68.0 cm, number of pieces from 18 to 97 per transect, and decay class evenness from -1.21 to -0.19 (where 0 is perfectly even).

3.1 | CWD habitat quality index

Only 3% of sites had an index score greater than 80, 16% greater than 60 and 44% greater than 50. This suggests that

very high scores are rare in this system, and scores ≥ 60 can be considered to indicate high CWD quality.

The app to calculate index scores is available at https://laura-vangalen.shinyapps.io/CWD_habitat_quality_index/, and can be operated using a web browser. The app calculates index scores for wet eucalypt forests based on our reference data set, although the option is available to upload alternative reference data sets for other forest systems.

3.2 | CWD quality and forest maturity

Both the structural and floristic maturity metrics had significant ($p < .05$), but very weak, positive relationships with the CWD index ($R^2 = .089$ and $R^2 = .073$, respectively;

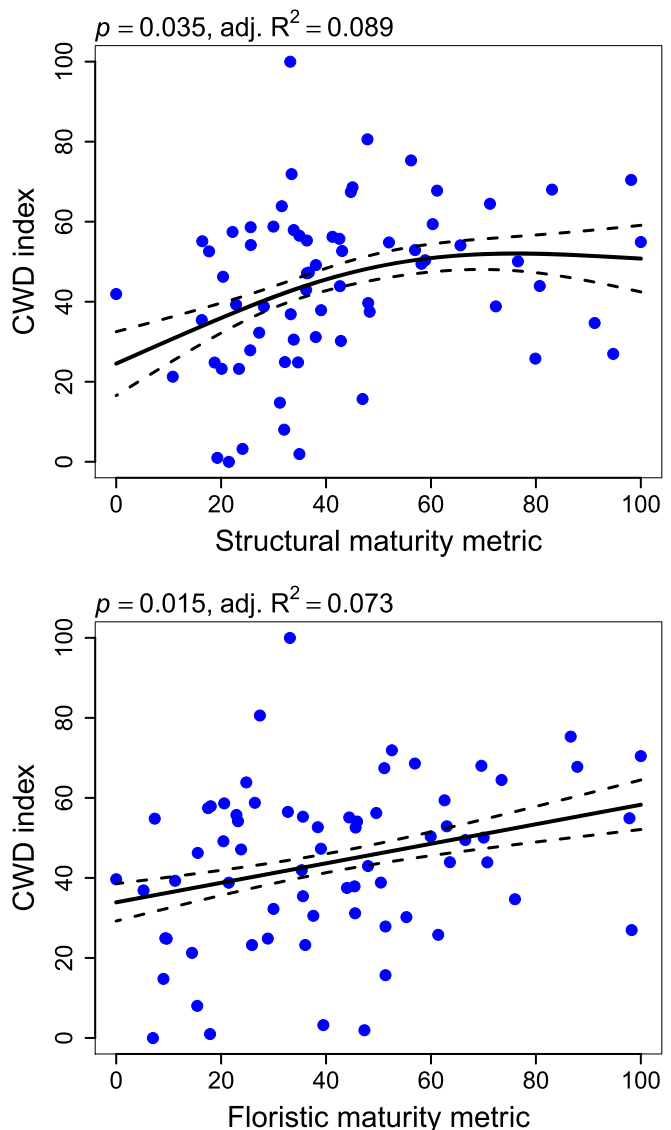


FIGURE 1 Relationship of the CWD index with the structural and floristic maturity metrics from van Galen et al. (2018). The solid line shows the curve of best fit (calculated from the GAM), and dashed lines show upper and lower standard errors for the fitted curves

Figure 1). Decay class evenness was weakly related to structural maturity ($p < .001$, $R^2 = .320$) and decay class evenness and number of pieces were very weakly related to floristic maturity ($p = .025$, $R^2 = .060$ and $p = .047$, $R^2 = .043$, respectively; Figure 2). Thus, although CWD habitat quality is related to forest maturity, the latter is not a proxy for CWD habitat quality.

3.3 | Current versus future quality and the effect of harvesting

The stand structural variables relating to future CWD input exhibited clear hump-shaped relationships with the CWD index scores (Figure 3): sites with the highest numbers of old-growth eucalypts and largest stand basal areas were those with medium levels of current CWD habitat quality. This relationship was strongest within wildfire-regenerated sites (Figure 3). Wildfire-regenerated sites had significantly higher CWD index scores ($p = .003$), more old-growth eucalypts and larger stand basal areas ($p < .001$) than clearcut-regenerated sites.

4 | DISCUSSION

We have developed an index and app for calculating CWD habitat quality that is relevant in forest ecosystems worldwide. The metric can be used to assess the habitat quality of

forests for saproxylic biodiversity, and could be applied in forest inventory, environmental impact assessments, and for research and monitoring programs. For example, thresholds of minimum desirable CWD habitat quality could be established for management applications such as habitat retained in forest harvesting (Jonsson et al., 2006) or habitat created in restoration projects (Manning et al., 2013).

The weak relationship between CWD quality and forest maturity (Figures 1 and 2) strengthens previous arguments (Grove, 2002; Grove & Meggs, 2003) that focusing forest management strategies purely on mature forest values is insufficient for conserving saproxylic habitat. It should be noted that the CWD quality metric is not an index of forest maturity per se. While it incorporates two measures of log size that strongly relate to tree maturity, it also encompasses the number of CWD pieces, and the variance in decay class. This latter variable recognizes that fresh inputs of CWD can be just as important for providing saproxylic habitat as heavily decayed logs (Jonsell et al., 1998; Lachat et al., 2006). Limbs shed from large senescing trees can be an important ongoing supply of CWD in eucalypt forests (Killey, McElhinny, Rayner, & Wood, 2010), but self-thinning of younger trees likewise provides fresh CWD inputs.

The relationships we observed between the index and variables indicating future quality (Figure 3) suggests that CWD dynamics are related to some aspects of forest succession, but the weak relationship with the maturity metrics

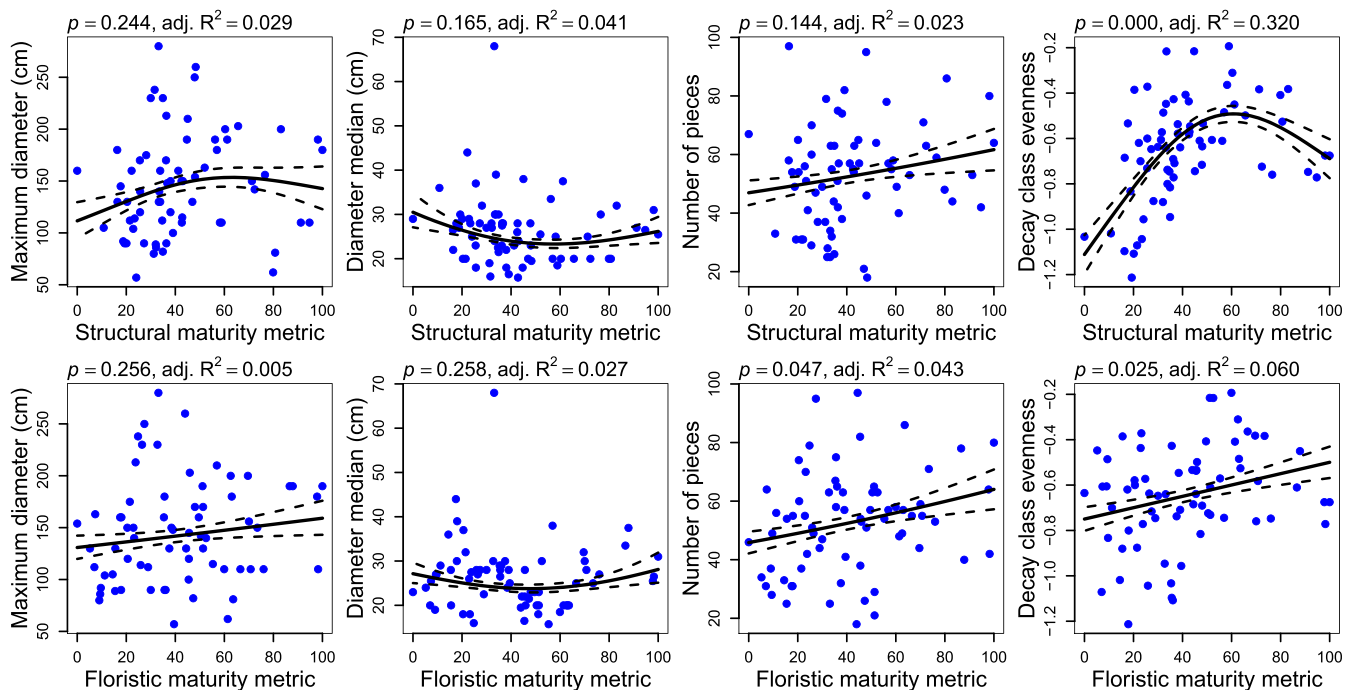


FIGURE 2 Relationship of the individual variables incorporated in the CWD index with the structural and floristic maturity metrics from van Galen et al. (2018). The solid line shows the curve of best fit (calculated from the GAM), and dashed lines show upper and lower standard errors. Variables that required transforming (see Methods) have been back-transformed for plotting

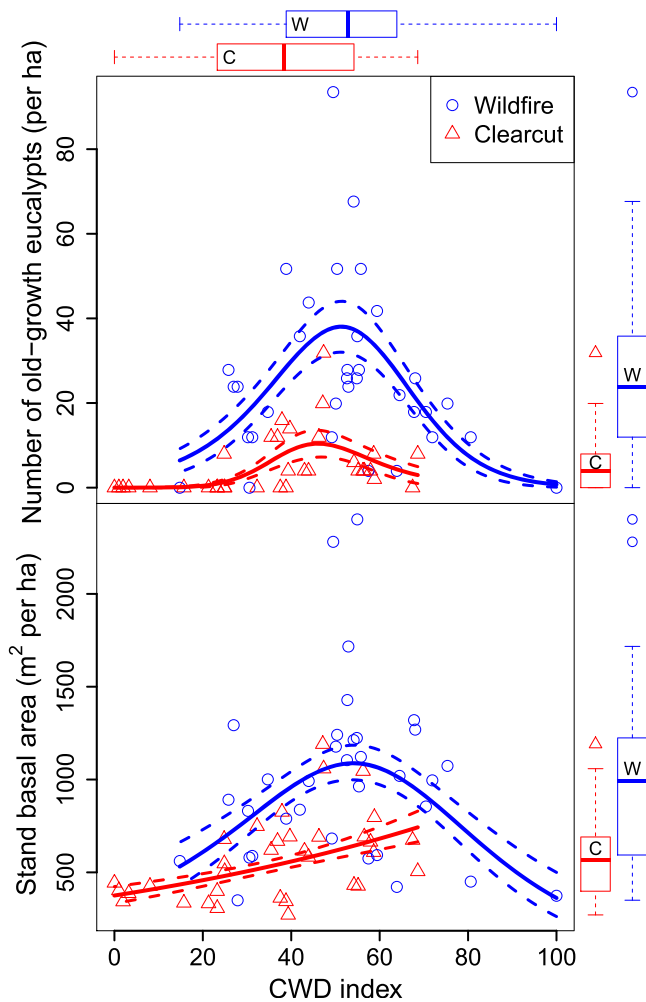


FIGURE 3 Relationship of the CWD index with the number of old-growth eucalypts and total stand basal area. The solid lines show the curves of best fit (calculated from the GAMs) and dashed lines show upper and lower standard errors for the fitted curves. Boxplots show the interquartile range and median, with whiskers extended to 1.5 times the interquartile range. W = wildfire, C = clearcut

shows that this relationship is not consistent across all aspects of forest maturation. Conserving high levels of standing structure, particularly large old-growth trees, is important for ensuring future CWD quality (Grove et al., 2009; Killey et al., 2010; Wardlaw et al., 2009), but mature structural and floristic attributes are poor proxies for aspects of current CWD quality. Thus, CWD needs to be considered alongside other stand attributes to make more informed management decisions.

We observed that for wet eucalypt forests, stands with the best current CWD habitat may not be those with the best CWD habitat in the future, with a hump-shaped distribution between current and potential future habitat (Figure 3). “U-shaped” relationships between CWD volume and forest age are commonly reported around the world (Feller, 2003;

Sturtevant, Bissonette, Long, & Roberts, 1997; Yan, Wang, Huang, Zeng, & Gong, 2007), and occasionally other types of relationships (e.g., inverse U-shape, continuous increases; Feller, 2003). In restoration projects, deliberately creating CWD can bring forward the conservation benefits of CWD habitat that otherwise might take centuries to develop (Manning et al., 2013). However, very little research has examined how current CWD quality relates to potential future quality; although Threlfall, Law, and Peacock (2018) observed CWD volume was weakly positively related to dead tree density but weakly negatively related to total tree density in eucalypt forests in eastern Australia. Additionally, very little research examines multiple elements of CWD quality.

The humped distribution is an important finding regarding the long-term conservation of saproxylic habitat, and may be due to two factors. Sites with few old-growth trees and low basal area could have low index scores due to lack of ongoing input of large CWD of varying decay stages, particularly if those sites contain clearcut-regenerated forest where most logs were removed during harvesting. Conversely, low levels of standing structure can occur in late-successional stages after the forest becomes sparse and most old-growth eucalypts die (Gilbert, 1959). In this case, previous old-growth trees at the site would have cumulatively contributed to CWD, leading to high index scores. In wet eucalypt forests, CWD can take more than 200 years to fully decompose (Grove et al., 2009), so conserving stands with high current quality could go a long way to conserve saproxylic species. Considering future quality may be particularly important in other systems where log decomposition rates are generally higher (Grove et al., 2009). Thus, for long-term management planning it is important to consider other stand structural variables as well as CWD index scores. Management practices that retain standing live and dead mature trees as habitat (Fedrowitz et al., 2014; Koch & Baker, 2011) could be integrated with CWD retention guided by use of our index to help ensure both good quality CWD now and in the future.

Silvicultural practices are often designed to mimic elements of natural disturbances to reduce their impact on species. The predominant harvesting method in wet eucalypt forests is clear-cutting followed by high intensity fire to mimic natural stand-replacing wildfires (Hickey & Wilkinson, 1999). While methods such as clear-cutting may mimic some important aspects of stand-replacing wildfires (Baker, Richardson, Seeman, & Barmuta, 2004; Hickey, 1994), numerous studies have observed differences in CWD characteristics between managed and unmanaged forests (e.g., Banaś, Bujoczek, Zięba, & Drozd, 2014; Grove & Stamm, 2011; Müller, Hothorn, & Pretzsch, 2007; Sippola et al., 1998; Thauvin et al., 2010; Threlfall et al., 2018). Our results also

indicated that unmanaged wildfire-regenerated sites had significantly better quality CWD and better potential future quality (more old-growth eucalypts and higher stand basal area; Figure 3) than clearcut-regenerated sites. It is important to note that in our study clearcut sites were generally younger (20–56 years old) than wildfire sites (at least 50 years old), which may have contributed to some of the differences. However, without ongoing inputs of CWD in clearcut sites, the CWD habitat quality would be further diminished when they are of similar age to wildfire sites. Previous modeled and field comparisons indicate that wildfires result in higher volumes of CWD than clearcuts (after the initial post-harvest spike; Grove & Stamm, 2011; Thauvin et al., 2010). Additionally, these studies observed that the distribution of decay classes remained relatively even in wildfire-regenerated stands, but early decay stages became rare over time after clear-cutting. Extensive fuel wood harvesting would be expected to further exacerbate the differences between harvested and naturally disturbed stands (Riffell et al., 2011). Spatial and temporal connectivity are key factors influencing community diversity (Grove & Meggs, 2003), so management practices must ensure that these do not become excessively altered.

The paucity of sites with index scores greater than 80 indicates that sites with very high habitat quality are sparse in this system. Therefore, considering sites with scores of 60 or above as high quality may be useful. Tasmanian wet eucalypt forests have particularly high levels of CWD compared to other forests around the world (Woldendorp & Keenan, 2005), so sites with mid index scores may still provide relatively good habitat. Managers should decide what constitutes sufficient habitat quality based on their required outcomes. The web app provides information about the relative contribution of the four variables to the overall index scores, which may help with these decisions.

In conclusion, our study supports arguments that focusing management strategies on conserving mature forest values does not necessarily lead to adequate conservation of saproxylic habitat, illustrating the importance of including CWD in management protocols. Comparison of index scores with structural variables indicating potential future CWD quality show that stands with the best current quality may not have the best quality in the future. Therefore, for ensuring successful long-term saproxylic conservation, both current CWD quality and other stand structural variables should be considered. We present a CWD habitat quality index that could be incorporated into current management protocols to inform better management decisions for the conservation of saproxylic species. This provides a simple means of collating important CWD attributes to help facilitate ecologically sustainable forest management. While the index presented here was developed for

Tasmanian wet eucalypt forests, our method could be easily applied to forest systems around the world. This would need to be constructed around the natural CWD formation and decay dynamics in the system and region-specific reference data sets. The app allows other reference data sets to be uploaded when required. Line intersect transects are assessed as part of standard forest inventories in some regions (Woodall et al., 2008), so developing reference data sets for those regions should not be difficult.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

All authors contributed to the development of ideas, analyses and writing the manuscript. L.G.v.G collected the data and led the analyses and writing.

DATA ACCESSIBILITY

All data supporting this research is provided as supplementary information accompanying this paper.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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